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PARASITISM OF BARRENS BUCK MOTH *HEMILEUCA MAIA* DRURY IN EARLY AND LATE SUCCESSIONAL PINE BARRENS HABITATS

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ABSTRACT. Barrens buck moth, *Hemileuca maia*, is predominantly associated with early successional pine barrens dominated by scrub oak, *Quercus ilicifolia*. To determine if *H. maia*'s association with these open habitats within pine barrens on Cape Cod is due to reduced rates of parasitism, we compared mortality of *H. maia* larvae on scrub oak in early successional right-of-way habitat and climax pitch pine communities. We established experimental populations of *H. maia* in both habitats and assessed parasitism in two consecutive years. Contrary to our hypothesis, parasitism by the introduced generalist tachinid *Compsilura concinnata* did not vary among habitats in either year, nor did it cause significant mortality to *H. maia* larvae in either year. In 2002, mortality from the native hymenopteran *Hyposoter fugitivus* was significantly reduced in forest plots and in 2003 parasitism by the native tachinid *Leschenaultia fulvipes* was significantly higher in power line right-of-way plots. Parasitism rates in both years did not appear high enough to underlie the documented differences in habitat selection by buck moth.

Additional key words: Habitat heterogeneity, *Compsilura concinnata*, enemy-free space, natural enemies, Cape Cod, *Quercus ilicifolia*.

The distribution of many insect herbivores is at least partially a function of the threat imposed by natural enemies, either through direct attacks or by causing herbivores to seek out niches that act as refuges (Schultz 1983, Jeffries & Lawton 1984, Price 1987, Bernays & Graham 1988, Stamp 2001, Williams *et al*. 2001). Life history strategies that avoid peak periods of natural enemy abundance are likely to be favored by natural selection (Schultz 1983, Jeffries and Lawton 1984, Tauber *et al*. 1986, Lill 2001). These include changes to life history attributes such as development and phenology, which minimize exposure to natural enemies (Bernays & Graham 1988, Mira & Bernays 2002), chemical defenses (Denno *et al*. 1990, Stamp 2001), or utilization of specific positions within a habitat where pressure from natural enemies is reduced (Stamp & Bowers 1988, Stamp & Bowers 1991). Habitat structure may also play an important role in providing enemy-free space for many insects (Ohsaki & Sato 1990).

Barrens buck moth (*Hemileuca maia* Drury, Saturniidae), is a univoltine, diurnal species with special concern status in the state of Massachusetts (Nelson 2002, NHESP 2007) and is considered to be rare throughout most of northern New England (Boettner *et al*. 2000). It appears to be restricted to isolated, remnant pitch pine (*Pinus rigida* Mill.) – scrub oak (*Quercus ilicifolia* Wangenh.) barrens in the northeastern United States, a habitat threatened by multiple anthropogenic factors (Tuskes *et al*. 1996, Wagner *et al*. 2003, Barbour *et al*. 1998). Furthermore, the distribution of *H. maia* within pine barrens is concentrated in only a few habitats (Schweitzer 1983, Tuskes *et al*. 1996, Nelson 2002) despite the occurrence of its primary host plant, scrub oak, across a much larger geographic range. Northeastern populations of *H. maia* appear to be particularly abundant in anthropogenically-created, early-successional habitats including road margins and power line rights-of-way (Schweitzer 1991, Nelson 2002, S. Haggerty, pers. com.). The occurrence of *H. maia* in early successional habitats and its apparent absence in later successional forests has not previously been explained. One possible factor is the effect of natural enemies, which is thought to increase with habitat complexity (Langellotto & Denno 2004). The sparse vegetation and lack of stratification in early successional areas may offer enemy-free or at least enemy-reduced space for *H. maia*.

Numerous parasitoids attack the larvae of *H. maia* (Schaffner & Griswold 1934, Arnaud 1978, Krombein *et al*. 1979, Piegler 1994, Boettner *et al*. 2000). Common species include *Hyposoter fugitivus* (Say) (Ichneumonidae) and *Meteorus autographae* (Muesebeck) (Braconidae) and the tachinid *Leschenaultia fulvipes* (Bigot) (Schaffner & Griswold 1934, Boettner *et al*. 2000). The non-native tachinid

Compsilura concinnata (Meigen), an important threat to saturniids (Boettner *et al.* 2000, Kellogg *et al.* 2003) also parasitizes *H. maia* and the congener *H. lucina* (Stamp 1990, Boettner *et al.* 2000).

Although the diversity of parasitoids attacking *H. maia* has been documented, little effort has been made to quantify stage-specific mortality, which is instrumental in understanding population dynamics. When stage-specific mortality has been determined, it has focused only on early-instars (Boettner *et al.* 2000). Thus, the impact of parasitoids on later instars and pupae is unknown.

Our study quantified mortality sources for *H. maia* larvae and pupae in two distinct habitats within pitch pine - scrub oak barrens on Cape Cod, MA. Research focused on three separate but related hypotheses: (1) the spatial distribution of *H. maia* is influenced by parasitoids, (2) habitat structure alters the species composition of the parasitoid fauna, and (3) habitat structure influences the level of mortality caused by parasitoids. Based on these hypotheses, we tested two predictions: (i) the community of parasitoids attacking *H. maia* will be richer in late successional (closed-canopy forest) habitat as opposed to early successional (open-area) habitat, and (ii) *H. maia* mortality from parasitoids will be reduced in early-successional habitat.

MATERIALS AND METHODS

Site description. Our study site was located on the peninsula of Cape Cod in Massachusetts, USA. The study area was located within Cape Cod National Seashore in Barnstable County, and consisted of a 9 km area running north-south throughout a portion of the outer Cape. The area included a 40 m wide power line right-of-way bounded by a mature closed-canopy pitch pine forest to the east, and a paved bike trail to the west. The power line right-of-way was mechanically cut every 3–4 years, perpetually maintaining an early successional habitat. A buffer corridor of pitch pine, scrub oak, black oak (*Quercus velutina* Lam.), black cherry (*Prunus serotina* Ehrh.), and beach plum (*Prunus maritima* Marsh) was left intact parallel to the bike trail. The vegetation within the power line right-of-way was cut to a height of <10 cm in 2002. By the summer of 2003, scrub oak, black oak, pitch pine, cherry and beach plum had re-sprouted from the stumps or roots. Pitch pine was the dominant tree in the closed canopy forest. Black, scarlet (*Q. coccinea* Muenchh.) and scrub oak were also present as canopy and subcanopy trees. Temperature and light intensity were significantly higher in the power line corridor than in the closed-canopy forest (JAS unpublished).

Larval mortality. 2002 – Baseline data on parasitism were collected in 2002 in a 1.5 km portion of the main 2003 study area. First instar *H. maia* larvae were deployed in the field for 12 days on scrub oaks within three distinct habitats. Each plot consisted of one scrub oak. Three plots were located within closed canopy forest (FOREST), three were located along the forest / power line border (EDGE), and three were within the power line / bike trail buffer (BUFFER). The central portion of the power line corridor was not useable, as it had been mowed the previous winter. Sixty-five first instar larvae were released at each plot. Larvae were monitored and counted on a daily basis, and were retrieved after 12 days to prevent dispersal losses which increase in late instars. Larvae were retrieved as late second and early third instars, then reared indoors until pupation or until parasitoids issued. A control population was reared entirely in the lab. The control group was collected as late first instars and thus a small proportion were parasitized. To account for the base level of parasitism within the control group, Henderson-Tilton's formula for unequal populations was employed prior to analysis (Henderson 1955).

In addition, five naturally occurring larval clusters were collected from the buffer area. Most of these aggregations consisted of third and fourth instars. All larvae were collected and reared under the same conditions as experimental larvae.

For indoor rearing, groups of 25–30 larvae were placed in 31 cm x 23 cm x 10 1/2 cm ventilated plastic boxes and maintained indoors at room temperature. Larvae were provided with fresh scrub oak foliage every 2–3 days. Florists' aqua-picks were used to keep foliage fresh. Fifth and sixth instar larvae were transferred to disposable 0.47 L plastic cups (4–6 larvae / cup) with 5 cm of potting soil for pupation, and were fed as above. Pupae were transferred to a 0.75 m^2 wooden frame rearing box covered with 2.5 mm wire mesh. The box was filled with 5 cm of soil and kept at room temperature until adult emergence in September and October. Adults mated within the box, and red oak (*Q. rubra* L.) branches were placed inside to provide females with oviposition surfaces. Eggs were kept outdoors in aerated plastic containers throughout the winter.

2003 – In early May, overwintered egg masses were moved indoors and kept refrigerated at a temperature of ~3°C until ready for use in field experiments. Hatching commenced on 31 May, with the majority of the egg masses hatching by 6 June, coinciding with bud break and egg hatch in natural populations. All larvae were hatched by 14 June.

Twelve plots were selected throughout the 9 km study area in locations where naturally-occurring clusters of

H. maia were observed in 2002. The area was divided into six 1.5 km sections with two plots in each section. All sections contained one plot along the power line corridor and one plot within the closed canopy forest. This was done to ensure equal dispersion of treatments (Hurlbert 1984). The location of each plot was randomly selected within the habitat, with two restrictions: (i) plots were at least 50 m from one another, and (ii) forest plots were at least 40 m from the eastern edge of the power line corridor. Each plot consisted of one scrub oak tree. Small (< 3 m tall) scrub oaks similar to those chosen by females in natural populations were selected (Sferra & Dunwiddie 1990, Schweitzer 1991). In instances where an appropriate tree could not be located at the randomly selected distance, the nearest tree located due south of that location was chosen.

Approximately 50 first instar *H. maia* larvae were deployed on each tree; this number is at the low end of aggregations in natural populations but is within the range of naturally occurring egg masses (Nelson 2002). To prevent dispersal losses, wandering larvae were confined to the immediate vicinity of scrub oak trees with 25 cm high aluminum flashing ground barriers (*H. maia* can not ascend aluminum flashing) placed around each tree outside the drip-line, approximately 1.75 m in diameter. Flashing was countersunk approximately 10 cm into the ground so that larvae could not go underneath it. Tall vegetation, sticks, leaves, and other debris were cleared from the inner perimeter to prevent larvae from climbing on other materials to reach the top of the flashing. When necessary, oak branches were trimmed or tied together so that the drip-line remained within the flashing perimeter. Small-scale experiments conducted in 2002 indicated that the ground barrier method causes minimal short-term disturbance to the habitat yet was completely successful in preventing larvae from wandering.

Mesh bird exclosures were placed around each tree on which larvae were deployed, enclosing both the tree and the aluminum flashing barrier. Exclosures were constructed using sections of 1.9 cm PVC pipes covered with 2.5cm netting (after Campbell *et al.* 1984). The exclosures eliminated bird predation but still allowed unfettered access by parasitoids. Comparison of plots with and without this type of exclosure indicated that neither diversity nor abundance of parasitoids attacking *H. maia* in New York was affected (DP unpublished).

Larvae were counted at least every other day. After a period of 7–10 days (approximately the length of an instar) the larvae were retrieved and replaced with 50 laboratory-reared larvae of the next instar. This time period varied based on weather conditions, as larvae developed more quickly during periods of warm, dry weather. This sequential deploy, collect, and replace technique (Boettner *et al.* 2000) was continued until the fifth instar, and was used to quantify mortality of *H. maia* throughout each of its larval stages. To limit the already large number of larvae required for this method, fifth and sixth instars were considered together, and were deployed for a period of 11 days. Retrieved larvae were reared in the laboratory until adults emerged or parasitoids issued.

Late stage *H. maia* lose their gregariousness and complete their development as solitary larvae (Tuskes *et al.* 1996, Nelson 2002). To account for this behavioral change, fewer fifth instar larvae were deployed on each tree but the number of trees they were deployed on was increased. Three trees in each habitat, including the original plot tree, were selected in every 1.5 km section. These additional trees were selected due north and due south of each original plot tree at a minimum distance of 20 m from the original. Ten larvae were placed on each tree. As these trees were in relatively close proximity to one another, and because the additional trees were chosen based on the location of the original plot tree, they were considered together as one plot in all analyses.

Pupal mortality. In 2003, we deployed a total of 120 *H. maia* pupae in marked locations in both forest and power line habitats. At each of the 12 plots, ten pupae were buried approximately 5 cm beneath the soil, approximating natural depths (Nelson 2002). Pupae were buried in two rows of five in a north-south direction, each a distance of 0.5 m from one another. The sex of each pupa was recorded. The location of each pupa was marked with a discrete 40 cm steel rod so it could be relocated in the future. The sex of pupae was determined prior to being buried on August 4 and 5. Half of the pupae buried at each plot were enclosed in small cylindrical cages made from 6 cm^2 sections of 0.64 cm galvanized hardware cloth. One pupa was enclosed in each cage. This design eliminated small mammal predation but allowed access to invertebrate predators. All plots contained three caged and three uncaged males, and two caged and two uncaged females. Pupae were retrieved on Sept. 21. A pupa was considered to have been depredated if it was not retrieved from the marked release location, or if it was damaged.

Statistical Analysis. 2002 Larval mortality: Each different mortality source was analyzed separately using the Kruskal-Wallis nonparametric test. Only larvae that were retrieved from the field were included in the analysis, since we could not determine causes of mortality for missing larvae. Two plots, one edge plot

Table 1. Mortality of *H. maia* larvae collected from naturally-occurring populations on Cape Cod, MA in 2002. Values indicate the percentage of parasitized larvae from the different parasitoid species. CoCo = *Compsilura concinnata*, HyFu = *Hyposoter fugitivus*, MeAu = Meteorus autographae, and LeFu = *Leschenaultia fulvipes*.

Site	Date	N	Instar	CoCo	HyFu	MeAu	LeFu	Survival*
NP1	20 June	13	3	0	7.7	0	0	92.3
NP2	20 June	24	3/4	0	4.2	0	0	79.2
NP3	21 June	15	4	6.7	13.3	0	0	80.0
NP4	21 June	15	3/4	13.3	0	0	0	86.7
NP5	21 June	20	4	35.0	0	5.0	10.0	55.0

*Value reflects total survival and includes mortality from non-parasitoid sources.

and one buffer plot, were excluded from the analysis because no larvae were recovered. Only descriptive statistics are presented for the parasitism occurring in natural populations.

2003 Larval mortality: Analysis was conducted using a series of t-tests. All instars and mortality sources were analyzed separately. Cumulative mortality was calculated using the equation described in Elkinton *et al.* (2006):

$$Cumulative\ Mortality = 1 - (1-m_1)(1-m_2)(1-m_3)...(1-m_i)$$

where m_i is the fraction of larvae dying during instar i.

2003 Pupal mortality: Pupal mortality data were analyzed as a split-split plot to examine the interactions among habitat, sex, and treatment (cage vs. no cage) for parasitism and predation.

RESULTS

Larval Mortality. In 2002, three species of parasitoids were recorded from experimental populations of *H. maia* larvae: *Meteorus autographae*, *Hyposoter fugitivus*, and the exotic *Compsilura concinnata*. In addition to parasitism, several larvae succumbed to a *Beauvaria sp.* fungus, and others died of unknown causes. Parasitism by *H. fugitivus* was significantly higher in buffer plots (df = 2, p=0.009). There were no other differences in the parasitoid fauna among the three different habitat types (Figure 1).

The 'control' population experienced parasitism from three of the parasitoids, albeit in very low numbers. Control larvae succumbed to 1.7% mortality from *C. concinnata*, 5.0% mortality from *M. autographae*, and 5.0% mortality from *H. fugitivus*, all of which emerged during or prior to the third instar. This indicates that all three parasitoids are capable of attacking first instar *H. maia* larvae.

Naturally occurring *H. maia* larvae were collected primarily as late third and fourth instars, and were consequently exposed to parasitism for a greater period of time than the experimental populations. These larvae had moderate levels of *C. concinnata* parasitism and were also parasitized by a fourth species not found in the experimental populations, the native tachinid *Leschenaultia fulvipes* (Table 1). There was little parasitism by *M. autographae* and *H. fugitivus* in natural populations, although it is likely that these species parasitized and killed early instar *H. maia* larvae before they were collected.

Parasitism was markedly lower in 2003 than in the previous year (Table 2). The three species of parasitoids recovered from the 2002 experimental populations were present again in 2003, though in much lower numbers. In addition, *L. fulvipes* was recovered from late-instar experimental *H. maia* larvae in 2003. As many as eight individual *L. fulvipes* puparia were obtained from a single *H. maia* host. Additional sources of larval mortality included a *Beauvaria sp.* fungus, a virus and unknown factors.

With the exception of *L. fulvipes* parasitism of fifth and sixth instar *H. maia* larvae, where parasitism was significantly higher in power line plots (t_5=2.60, p=0.048), all other comparisons for all instars were not significant. If a correction for multiple tests is conducted (adjusted alpha=0.0024), then even the difference in *L. fulvipes* parasitism of fifth and sixth instars becomes insignificant. While some advocate the use of corrections for multiple tests (Peres-Neto 1999), others maintain strong arguments against adjusting the alpha level (Gotelli & Ellison 2004), and we leave the final determination to the reader's discretion. None of the parasitoids, either acting alone or taken as a whole, caused high levels of mortality to *H. maia* larvae, which had uniformly high survival.

Comparisons of cumulative mortality rates also indicated that parasitism by *L. fulvipes* in power line plots was significantly higher than in forest plots (t_6=2.49, p=0.047). Mortality inflicted by the other parasitoid species did not differ between the different habitats (Figure 2).

Pupal mortality. The test for interactions between habitat, sex, and treatment (cage vs. no cage) and all combinations of these was not significant. The test for

Table 2. Two-tailed test results for 2003 *H. maia* larval mortality study on Cape Cod, MA, comparing power line populations to forest populations. Values indicate the percentage of parasitized larvae from power line (POW) and forest (FOR) populations. Where mortality sources are marked (°), there was insufficient information to conduct statistical analyses, as only 1 of 12 sites showed evidence of mortality from that source. CoCo = *Compsilura concinnata*, HyFu = *Hyposoter fugitivus*, MeAu = *Meteorus autographae*, LeFu = *Leschenaultia fulvipes*.

Mortality	Instar	POW	FOR	DF	T	P
CoCo	1	0	0	-	-	-
HyFu	1	0	0	-	-	-
MeAu	1	0	1.55 ± 0.98	5	-1.58	0.175
LeFu	1	0	0	-	-	-
Fungus°	1	0	0.68 ± 0.68	-	-	-
Virus	1	6.02 ± 2.2	8.47 ± 2.6	9	-0.71	0.495
Unknown	1	8.25 ± 3.5	8.75 ± 2.2	8	-0.12	0.906
Survival	1	85.79 ± 4.8	80.6 ± 2.8	8	0.94	0.376
CoCo°	2	0.35 ± 0.35	0	-	-	-
HyFu°	2	0	0.33 ± 0.33	-	-	-
MeAu°	2	0	0.38 ± 0.38	-	-	-
LeFu	2	0	0	-	-	-
Fungus	2	0.68 ± 0.43	0.33 ± 0.33	9	0.64	0.537
Virus	2	5.72 ± 3.1	5.48 ± 2.8	9	0.06	0.957
Unknown	2	6.75 ± 1.2	7.18 ± 1.1	9	-0.27	0.796
Survival	2	86.52 ± 3.2	86.3 ± 3.4	9	0.05	0.958
CoCo°	3	0	4.25 ± 4.25	-	-	-
HyFu	3	0	0	-	-	-
MeAu	3	0	0	-	-	-
LeFu	3	0	0	-	-	-
Fungus°	3	0	1.07 ± 1.07	-	-	-
Virus	3	0.8 ± 0.51	1.4 ± 0.68	9	-0.70	0.500
Unknown	3	3.6 ± 0.59	5.67 ± 0.73	9	-2.20	0.055
Survival	3	95.61 ± 1.0	87.62 ± 4.8	5	1.62	0.166
CoCo°	4	0	4.87 ± 4.87	-	-	-
HyFu	4	0	0	-	-	-
MeAu	4	0	0	-	-	-
LeFu	4	1.15 ± 0.51	0.67 ± 0.67	9	0.57	0.580
Fungus	4	3.67 ± 1.7	1.03 ± 0.71	6	1.40	0.210
Virus	4	1.9 ± 1.1	2.33 ± 1.5	9	-0.23	0.821
Unknown	4	4.37 ± 2.0	6.78 ± 2.3	9	-0.80	0.443
Survival	4	88.92 ± 3.8	84.33 ± 7.0	7	0.58	0.581
CoCo	5/6	0	3.58 ± 2.4	5	-1.49	0.196
HyFu	5/6	0	0	-	-	-
MeAu	5/6	0	0	-	-	-
LeFu	5/6	19.2 ± 6.0	2.98 ± 1.6	5	2.60	0.048
Fungus	5/6	3.33 ± 2.27	0	5	1.47	0.203
Virus°	5/6	0	0.55 ± 0.55	-	-	-
Unknown	5/6	2.87 ± 1.6	3.65 ± 1.3	9	-0.39	0.709
Survival	5/6	74.65 ± 7.5	89.27 ± 4.1	7	-1.72	0.129

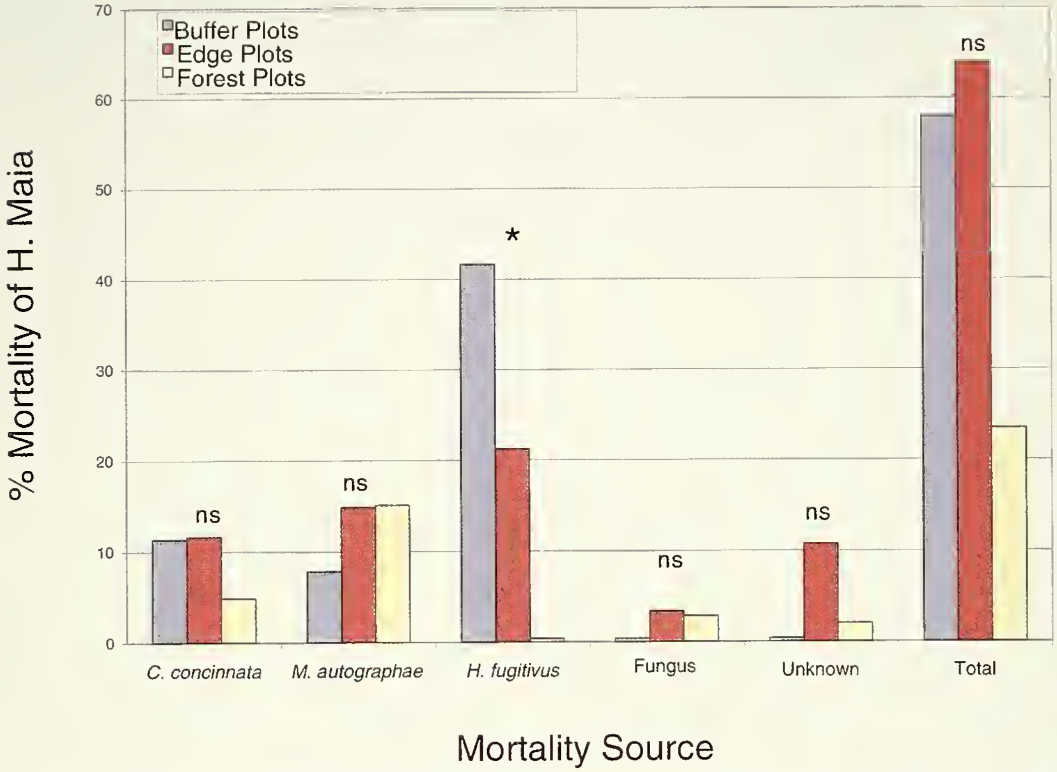

Fig. 1. Mortality of *H. maia* larvae on Cape Cod, MA in 2002. Mortality was calculated using Kruskal-Wallis nonparametric tests. A notation of 'ns' indicates that the comparison is not statistically significant at alpha 0.05. An asterisk (*) indicates a statistically significant comparison at alpha 0.05.

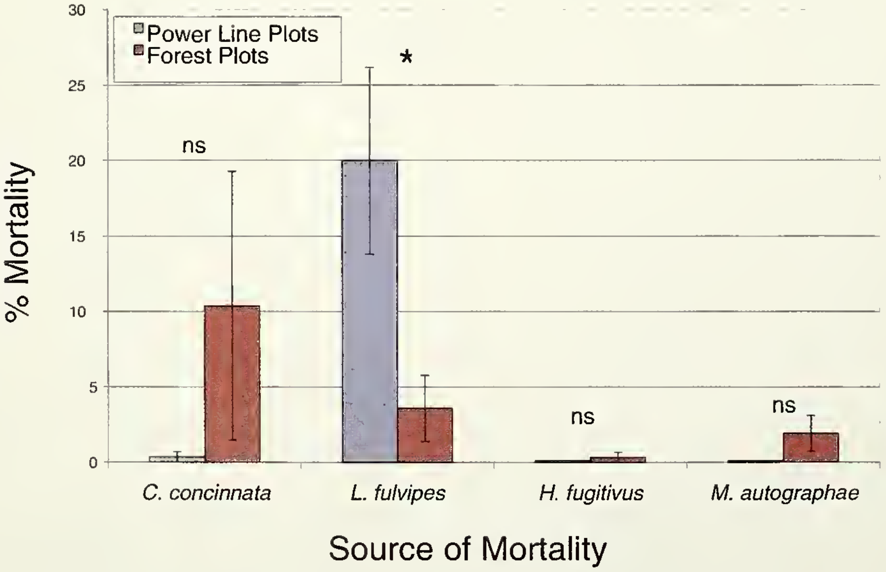

Fig. 2. Mean cumulative mortality (±SE) of *H. maia* larvae by parasitoids in 2003 on Cape Cod, MA. A notation of 'ns' indicates that the comparison is not statistically significant at alpha 0.05. An asterisk (*) indicates a statistically significant comparison at alpha 0.05.

differences between habitat and sex was also not significant. There was a significant difference between the predation of caged and uncaged pupae (t_1=24.21, p=<.0001), with 5.8 ± 8.8% (mean ± SE) of caged pupae and 38.4 ± 21.5 (mean ± SE) of uncaged pupae depredated. With one exception, all predated pupae were simply missing. In only one instance was a caged pupa eaten, presumably by an insect predator. We found no parasitism of either caged or uncaged pupae.

Discussion

Four species of parasitoids were reared from *H. maia* on Cape Cod during the two-year study. *Meteorus autographae* and *H. fugitivus* were primarily associated with early instar *H. maia* larvae. *Leschenaultia fulvipes* was not recovered from the experimental populations in 2002, which spanned only the first three instars. *Leschenaultia fulvipes* did occur in wild populations of late instar *H. maia* larvae in 2002, and again in late-instar experimental *H. maia* larvae in 2003, suggesting that *L. fulvipes* is predominantly associated with later instar *H. maia*. However, extensive parasitism by *L. fulvipes* in early instar larvae has been frequently observed in other *Hemileuca* populations (J. Tuttle, pers. com.). While it is possible that *L. fulvipes* parasitized and killed their early instar hosts before they were collected as 3rd and 4th instars, it should be noted that *L. fulvipes* was not represented in the control population.

The recovery of *Meteorus autographae* from *H. maia* is a new host record. Several previously collected specimens identified as *M. hyphantriae* from Plymouth and Brewster Counties in Massachusetts also were identified as *M. autographae*. We suggest that *M. hyphantriae* records from *H. maia* in old collections be reexamined for possible misidentifications, because many historic records appear to be from the same region (S. Shaw, pers. com.).

The tachinid *Compsilura concinnata* was also more prevalent in late-instar *H. maia*, consistent with prior observations with other Lepidoptera (Webber & Schaffner 1926, Burgess & Crossman 1929, Boettner *et al.* 2000, Kellogg *et al.* 2003). However, in 2002, *C. concinnata* was reared from second and third instars, and on one occasion even attacked a first instar larva. Although most *C. concinnata* larvae successfully emerged from smaller *H. maia* hosts and formed puparia, 14% of these puparia died, and adults that did emerge were half the size or less of adults emerging from puparia reared from late instars. Significant fitness costs may be incurred by flies attacking smaller individuals (e.g., Raupp & Denno 1983, Reavey 1993). Further, only one *C. concinnata* puparium was produced from each parasitized early instar larva in 2002, while in 2003 multiple emergence occurred in 38.5% of larvae, with as many as five *C. concinnata* produced from a single host.

The 2003 study was designed to specifically assess parasitism of late-instar larvae. While our observations accurately reflect the mortality inflicted on *H. maia* larvae in 2003, this may not be representative of all years. In other years, our study (2002) and those of others (Boettner *et al.* 2000) have shown higher rates of parasitism. However, a similar study in New York's Albany Pine Bush in 2005 found no parasitism by *C. concinnata* and very low parasitism by hymenopterans (DP and B. Hoven, unpublished data). In that study, only *L. fulvipes* was common.

The apparent greater abundance of *H. maia* in open, early successional habitats like powerline right-of-ways does not appear to be a function of changes in parasitoid pressure. There was some evidence that parasitoid species varied spatially among habitats based on the high percentage of *H. fugitivus* recovered from larvae in buffer plots in 2002 and the decreased rate of parasitism by *L. fulvipes* in power line plots in 2003, but all other comparisons were not significant. However, parasitism is but one of several biotic factors that may influence *H. maia* distribution. The abundance of predators, the distribution and quality of host plants, fire management, and microclimate conditions are all factors that may act alone or in combination to affect the oviposition choices made by *H. maia* adult females. Microclimate may be of major importance and should not be overlooked. Increases in temperature and light intensity may enhance behavioral thermoregulation through the absorption of solar energy (Seymour 1974, Cornell *et al.* 1987, Klok and Chown 1999, Hunter 2000). This may be particularly important for *H. maia* larvae on Cape Cod, as these populations are at the extreme northern limit of their geographic range.

We recorded modest levels of mortality in the pupal stage, although it is unclear what effect, if any, this has on its overall distribution. While pupal mortality is common in many other insect species (e.g., Weseloh 1985, Gould *et al.* 1990, Fuester & Taylor 1996, Tanhuanpää *et al.* 1999, Hastings *et al.* 2002), we are unaware of additional studies that examine pupal mortality of *H. maia*. Thus, we cannot competently assess whether the mortality levels that we observed constitute significant losses for this species. There was no evidence of pupal parasitism in either habitat. There was also no evidence that predators prefer the larger female pupae to the smaller male pupae. A significantly greater number of uncaged pupae were depredated as compared to those in cages. This suggests that predation was caused by birds, mammals, and/or large insect predators, as the mesh cages were accessible to smaller invertebrates. In only one instance was there clear evidence that a small invertebrate predator consumed a caged *H. maia* pupa.

The lack of significant mortality from the introduced *C. concinnata* offers some hope for future management of *H. maia* because it suggests that populations can be enhanced through habitat protection and management. In contrast, management of several other species of threatened saturniids in the northeast may be thwarted by the dominance of this tachinid as a mortality factor. Our data do suggest that the well-documented decline in populations of many saturniids in the northeast may be due to more than one factor, and the role of *C. concinnata*, which has been proposed as a major contributor to the decline, will depend on the species in question.

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